

The biology of sympatric species of *Scintillona* (Bivalvia: Galeommatoidea) commensal with *Pilumnopus serratifrons* (Crustacea: Decapoda) in Moreton Bay, Queensland, Australia, with a description of a new species

Brian MORTON

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.
Email: prof_bmorton@hotmail.co.uk

Citation: Morton, B. 2008 12 01 The biology of sympatric species of *Scintillona* (Bivalvia: Galeommatoidea) commensal with *Pilumnopus serratifrons* (Crustacea: Decapoda) in Moreton Bay, Queensland, Australia, with a description of a new species. In, Davie, P.J.F. & Phillips, J.A. (Eds), Proceedings of the Thirteenth International Marine Biological Workshop, The Marine Fauna and Flora of Moreton Bay, Queensland. *Memoirs of the Queensland Museum — Nature* 54(1): 339–354. Brisbane. ISSN 0079-8835.

ABSTRACT

Two species of the galeommatid genus *Scintillona*, *S. cryptozoica* and *S. daviei* sp. nov. are sympatrically associated with the gallery-building pilumnid crab *Pilumnopus serratifrons* inhabiting clumps of the mussel *Trichomya hirsuta* on a seagrass-covered intertidal mudflat at Myora Springs, North Stradbroke Island, Queensland, Australia. The new species is described and compared with *S. cryptozoica*. Sympatry is not total: of the 100 galeommatid clusters examined, 40 of *S. cryptozoica* and 27 of *S. daviei* were species specific, and 33 were sympatric. Clusters of *S. cryptozoica* and *S. daviei* ranged in numbers from 1–25 and 1–7 individuals, respectively. Both species appear to be protandric consecutive hermaphrodites: the male component of the ovotestis dominated at shell length sizes of 1–3 mm (*S. cryptozoica*) and 1–2.5 mm (*S. daviei*), respectively; females ranged in shell length from 5–10 mm and 3–7.5 mm, respectively. Both species brood fertilised eggs in the outer demibranchs of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm. The relationship of both species with their host crab appears to be related to protection within its gallery and the provision of respiratory and feeding currents by virtue of its activities, and can thus be defined as commensalism. □ *Scintillona* species, Galeommatoidea, sympatry, *Pilumnopus serratifrons*, Pilumnidae, biology, commensal relationship.

Fourteen species of mangroves occur in south-eastern Queensland (Duke 2006), though only seven reach as far south as Moreton Bay, which is the southern limit for most species (Davie 1998). At Myora Springs on the northwest coast of North Stradbroke Island, the coastal fringe of mangroves mostly comprising *Avicennia marina*, *Aegiceras corniculatum* and *Rhizophora stylosa* gives way to an extensive area of mud that is colonised at mid-tidal levels by the seagrasses *Zostera capricorni*, *Halodule uninervis* and *Halophila ovalis*. As the tide recedes, the seagrass beds are seen

to be dotted with clumps of the hairy mussel *Trichomya hirsuta* (Lamarck, 1819), up to ~15 cm in diameter. This large, up to 65 mm shell length, mussel has a wide distribution encompassing South Australia, Tasmania and New South Wales to as far north as northern Queensland (Lamprell & Healy 1998). The mussel clumps sit in shallow depressions in the mud, and when turned over, sometimes possess small groups of small, white, translucent bivalves. Two species of the genus *Scintillona* Finley, 1927 [formerly attributed to *Varotoga* (Iredale, 1931)]

(Galeommatoidea Gray, 1840) occur sympatrically beneath the mussel clumps. From the clumps have been recorded a number of other species of invertebrates, including an alpheid shrimp, but their bases are almost exclusively occupied by the pilumnid crab *Pilumnopus serratifrons* (Kinahan, 1856). This crab creates galleries in its mussel clumps, and it is to the roofs of these that the two bivalves attach.

Scintillona cryptozoica (Hedley, 1917) has been recorded from New South Wales, but its sympatric congeneric is undescribed. This study is therefore a description of the new bivalve species as well as a study of the biology of the two species, including basic anatomy, the extent and intimacy of their sympatry, reproduction and the relationship with their host crab *Pilumnopus serratifrons*.

The Galeommatoidea comprises a highly diverse group of miniature, commensal bivalves that are associated with an equally wide range of marine invertebrate hosts (Boss 1965a) (although *Cycladoconcha amboinensis* (Spärck, 1931) is possibly parasitic within the oesophagus of synaptid holothurians). Galeommatooids can also be members of quite complex communities, for example, the tiny (1.7 mm shell length) *Jousseaumliella conchiarum* shares a gastropod shell with a sipunculan and a polychaete (Knudsen 1944). They are, however, rarely recorded as associates of crabs although they do live with, similarly commensal, pinnotherids in often highly complex associations with larger invertebrate hosts (Manning & Morton 1987; Morton 1988). The association between the two species of *Scintillona* to be described herein with *Pilumnopus serratifrons* is thus of especial interest, particularly with regard to their sympatry, the morphological adaptations they have, particularly of the mantle, and their expressions of sexuality that equip them for such a lifestyle.

Abbreviations. Institutions: Queensland Museum, Brisbane, Queensland (QM); Australian Museum, Sydney, New South Wales (AM); The Natural History Museum, London, UK. (NHM).

Shell and anatomical structures: A, Anus; AA, Anterior adductor muscle (or scar); ADT, Antero-dorsal tentacle; AT, Anterior tentacles; B, Byssal thread; DD, Digestive diverticula; ES, Exhalant siphon; F(H), 'Heel' of foot; F(T), 'Toe' of foot;

H, Heart; HT, Hinge tooth; I, Intestine; ID, Inner demibranch; ILP, Inner labial palp; K, Kidney; L, Ligament; LP, Labial palp; OD, Outer demibranch; OLP, Outer labial palp; OVT, Ovotestis; PA, Posterior adductor muscle (or scar); PDT, Postero-dorsal tentacle; PS, Pigment spot; PT, Posterior tentacles; R, Rectum; RM, Reflected mantle; S, Socket; SUBC, Supra-branchial brood chamber; U, Umbo.

MATERIALS AND METHODS

From 9–24 February 2005, daily visits were made during periods of falling tides to the mud flats at Myora Springs, Moreton Bay, North Stradbroke Island, Queensland. Here, the sea-grass covered mud flats are dotted with byssally bound clumps of the mussel *Trichomya liirsuta*. On each visit, the clumps were picked up, turned over and examined for the galeommatid bivalves of the genus *Scintillona*. Where these were seen, all individuals were collected and put into pre-numbered vials of seawater. The clumps were then broken apart gently and any other animal species associated with the *Scintillona* individuals collected and placed in numbered tubes. On return to the laboratory, the *Scintillona* individuals were separated into species, that is, *S. cryptozoica* and a sympatric new species. Shell lengths of all individuals were measured. All individuals of all species collected in association with the mussel clumps, and the two species of *Scintillona* were identified to the highest taxonomic category.

Both *Scintillona* species were examined anatomically. Some individuals were drawn, others were dissected to expose details of shell and hinge structure, and general anatomy. The ciliary currents of the organs of the mantle cavity of both species were examined under a binocular microscope and elucidated using carmine dissolved in seawater. Finally, all individuals were sexed into one or other of four categories, that is: i) females brooding fertilised eggs in their ctenidia; ii) unfertilised females; iii) individuals of indeterminate sex; and iv) males. Subsequently, two individuals of the new species of *Scintillona* were, following routine processing and gold sputter coating, examined using a scanning electron microscope (Jeol 820) at the University of Cambridge.

Table 1. Data on the population structure of *Pilumnopeus serratifrons* inhabiting the mussel (*Trichomya hirsuta*) clumps on the shore at Myora Springs, Moreton Bay, North Stradbroke Island, Queensland.

	Numbers	Mean carapace width (mm)	Range in carapace width (mm)	Nos of single individuals	Nos of M:F pairs	Nos of M:M pairs	Nos of F:F pairs
Males	45	7.3	3.5 – 14.5	32	5	4	1
Females	33	9.2	5.5 – 14.0	26	–	–	–
Gravid females	9 (of 33)	8.7	7.5 – 10.0	7	2	–	–

HABITAT NOTES

The clumps of *Trichomya hirsuta* have as their basis an empty oyster shell, *Saccostrea glomerata* (Gould, 1850), a valve of *Pinctada* cf. *fucata* (Gould, 1850), or *Isognomon ephippium* (Linnaeus, 1758) or that of a conspecific. The mussel clump so attached may comprise >30 individuals, and the hair-like periostracum that covers the posterior region of each individual's valves creates a matted covering to the byssally bound, compact mass. The bowl of mud in which each mussel clump sits, is not anaerobically black, but clearly aerated. When each mussel clump is turned over, typically the most obvious co-residents are the galeommatid bivalves. Other inhabitants of the galleries included the near ubiquitous occurrence of *Pilumnopeus serratifrons*, and either one or two individuals each of: i) *Alpheus* cf. *pacificus* Dana, 1852 (Caridea: Alpheidae); ii) *Phascolosoma* cf. *arcuatum* (Gray, 1828) and *P.* cf. *dunwichi* Edmonds, 1956 (Sipuncula); iii) *Paralepidonotus* cf. *ampulliferus* (Grube, 1878) (Annelida: Polynoidae); iv), *Favonigobius* cf. *lateralis* (Macleay, 1881) (Pisces: Gobiidae) and v) occasional representatives of four other species of Galeommatoida (the latter all sent to Dr. P. Middlefart, Australian Museum, Sydney).

NOTES ON THE *PILUMNOPEUS SERRATIFRONS* POPULATION

A total of 78 individuals of *Pilumnopeus serratifrons* was collected comprising 45 males (57.7%) and 33 females (42.2%). Nine females were gravid (27.3%). The mean carapace widths of male and female individuals of *P. serratifrons* were 7.3 mm and 9.2 mm, respectively. Interestingly, although all collected individuals were relatively small (ranging in carapace width from 3.5–14.5 mm), this species can reach about 28.0 mm in carapace width

(Davie 1989). However, much of the material recorded by Davie (1989: 130) in his taxonomic revision of the species was of similar size to that recorded here. It would seem possible that smaller individuals preferentially inhabit mussel clumps as well as other narrow cavities such as in rotting logs and amongst oysters (Davie, pers. comm.). The broader habitat of this species is 'in the lower estuary or on sandy mud flats, living under stones and debris resting on the substrate, from about half tide level to low water' (Davie 1989).

The majority of individuals (32 males and 26 females occurred singly, although five male/female, four male/male and one female/female pairs were identified. Of the nine gravid (egg bearing) individuals collected, seven occurred singly while two were partners in the male/female pairs (Table 1). Morton & Lutzen (2008) report upon the rhizocephalan *Loxothylacus spinulosus* Boschma, 1928, parasitising *P. serratifrons* in the *Trichomya* clumps.

TAXONOMY

Hedley (1917, pl. xvi, fig. 1 [animal]; pl. ii, fig. 40 [shell]) erected a new name, *Solecardia cryptozoica*, for a gregarious galeommatid species that lives in 'companies of a dozen or so' (p. 685) individuals underneath stones at low water in Middle Harbour, Sydney. Iredale (1931: 206) proposed the generic name *Varotoga* for this species, as he felt *Solecardia* was being too broadly used 'for any glassy oval shell'. Subsequently, Iredale (1936) described a second galeommatid occupying the burrows of the prawn *Crangon* from Bottle and Glass Rocks, Watson's Bay, Sydney. This was called *Ambuscintilla praemium* gen. nov., sp. nov., although the illustration (pl. xxi, fig. 4) is clearly identical with that of

Varotoga cryptozoica (Hedley, 1917, pl. ii, fig. 40). Dr P. Middelfart (pers. comm.) believes that Iredale probably did collect specimens of a new species (of *Varotoga*) but that he also appears to have mixed them with at least one specimen of *V. cryptozoica* which was used for the published figure. As the deposited type specimen in the Australian Museum also belongs to *V. cryptozoica*, *Ambuscintilla praemium* must be treated as a junior synonym of *V. cryptozoica*.

Under current usage, *Varotoga* is considered a junior synonym of *Scintillona* Finlay, 1927 (see Lamprell & Healy 1998: 152). Dr Peter Middelfart is currently undertaking a revision of the Galeommatidea, and believes there are good reasons to maintain *Varotoga* as a separate taxon. However, until his revision is published it seems more appropriate to use *Scintillona* for the present work.

GALEOMMATOIDEA Gray, 1840

Galeommatidae Gray, 1840

Scintillona Finlay, 1927

Scintillona Finlay, 1927: 465 [type species: *Spaniorinus zealandica* Odhner, 1924].

Scintillona daviei sp. nov.

(Figs 1, 2, 3, 4, 5 & 6)

Material Examined. HOLOTYPE: QM-MO77617, shell length 4.5 mm, sand flat in front of Myora Springs, Moreton Bay, North Stradbroke Island, Queensland, 9-24,02, 2005, B. Morton. PARATYPES: QM-MO77618,

shell length 4.0 mm, AM-C.454645, shell length 5.0 mm, AM-C.454646, shell length 5.0 mm, NHM 20060145, shell length 4.0 mm, NHM 20060146, shell length 4.5 mm, data as for holotype.

Etymology. The species is named after Peter Davie, Senior Curator (Crustacea), Queensland Centre for Biodiversity, Queensland Museum, Brisbane, Queensland, Australia, in gratitude for his endeavours in organising the workshop during which the material was collected.

Description. Small (< 7.5 mm shell length), approx. equilateral and equivalved. Holotype: shell 4.5 mm in length; almost as tall (4.0 mm) as long and laterally plump. Posterior valve face more inflated and pointed than the more marginally rounded anterior. Hinge line purple with an internal opisthodontic ligament and small anterior hinge teeth on both valves interlocking in a medial socket. Shell translucent with purple hinge.

Remarks. *Scintillona daviei* sp. nov. has a distinctive array of tentacles and papillae adorning the middle mantle folds that are reflected to mostly cover the shell except apically (Fig. 1). The mantle margin is dark red around the exhalant siphon and yellow/orange around the inhalant aperture. There are antero- and postero-dorsal tentacles above the inhalant aperture and exhalant siphon, respectively. There are two pairs of other tentacles anteriorly and one pair posteriorly. Smaller papillae adorn the outer (actually the inner) surface of the reflected middle mantle fold. All the tentacles and papillae are coloured a deep red/purple apically. Such an arrange-



FIG. 1. *Scintillona daviei* sp. nov.: holotype (QM-MO77617) illustrated in life from the left side.

Table 2. *Scintillona cryptozoica* and *Scintillona daviei*: a comparison of anatomical characters.

Character	<i>Scintillona cryptozoica</i>	<i>Scintillona daviei</i>
Maximum shell length	10.0 mm	7.5 mm
Shell length to height ratio	1 : 0.69	1 : 0.75
Hinge area	Translucent white	Purple
Hinge teeth	Single anterior tooth in left valve	Single anterior teeth in left and right valves
Anterior tentacle area	Anterior tentacle red plus two other pairs	Anterior tentacle purple/red plus three other pairs
Posterior tentacle area	Posterior tentacle red plus three other pairs	Posterior tentacle purple/red plus two other pairs
General mantle papillae	Numerous: scattered all over reflected mantle	Reflected mantle with inner ring of 12 pairs plus outer postero-ventral ring of five pairs
Pedal pigment spot	Absent	Present
Shell length of mature females	Females mature at > 5 mm	Females mature at > 3 mm

ment of tentacles and the purple hinge identifies the species.

According to Lamprell and Healy (1998) two species of *Scintillona* occur in Australian waters. These are *S. hyalina* (Deshayes, 1856) and *S. cryptozoica* (Hedley, 1917). The former is known only from the holotype in the collections of the Natural History Museum, London (BMNH 196791) and was collected in the Torres Strait but from an unknown habitat (see Lamprell and Healy, 1998, fig. 395). It is 14 mm long, equilateral and is elongately oval with a straight hinge line. It is clearly different from the much smaller, rounded, plump *S. daviei* sp. nov.

Scintillona daviei also differs from the only other known Australian species, *S. cryptozoica* (but with which it is sympatric, as this study will show), in a number of distinctive ways (Table 2). Firstly, not only is *S. daviei* smaller (<7.5 mm shell length) than *S. cryptozoica* (10 mm shell length), but it is also plumper, that is, the shell length to height ratio is 1:0.75, versus 1:0.69. Secondly, the hinge line and plate of *S. daviei* is always a distinctive purple and the arrangement of the hinge teeth between the two species is subtly different. There are, thirdly, distinctive differences in the arrangement of the tentacles and pallial papillae, but *S. daviei* also possesses a distinctive pigment spot in the

foot whereas *S. cryptozoica* does not. Differences between the species are further detailed more extensively under the headings 'Shell Structure and Anatomy' following.

Distribution. Known only from the type locality; sand flats in front of Myora Springs, Moreton Bay, North Stradbroke Island, Queensland, Australia.

SHELL STRUCTURE AND ANATOMY OF *SCINTILLONA DAVIEI*

The shell of *Scintillona daviei* sp. nov. is illustrated as a SEM image from the left side in Fig. 2A. It is translucent and covered in a thin (2 µm) periostracum. The umbo is tall and prosogyrous. The posterior face is more inflated and pointed than the narrower and more rounded anterior. Nevertheless, the species is approx. equilateral and equivalve. Internally (Fig. 3A), the anterior (AA) and posterior adductor (PA) muscles are of approximately equal sizes and are situated below the anterior and posterior hinge lines, respectively. The purple hinge plate is illustrated in Figs 2B, C and 3B, C. The ligament (Fig. 3, L) is situated posterior to the umbo (U) and there is an anterior hinge tooth (HT) in the left valve (Figs 2B & 3B). There is a similar hinge tooth in the right valve (Figs 2C, 3C, HT) and both abut each other but do not

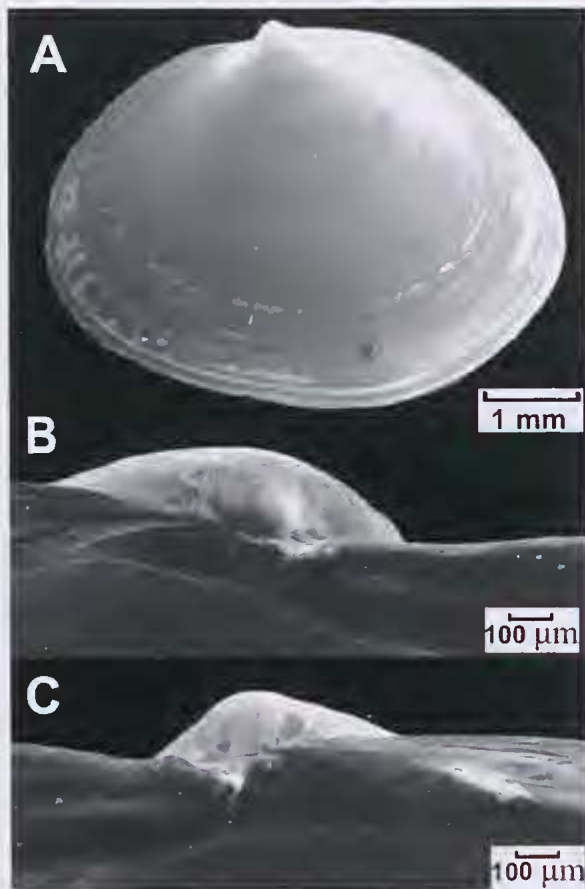


FIG. 2. *Scintillona daviei* sp. nov.: scanning electron micrographs of A, the external surface of the left shell valve; B, C, the internal structures of the left and right hinge plates, respectively.

interlock. There is a medial socket (S) directly beneath the umbo.

A mature individual of *Scintillona daviei* is illustrated in life position in Fig. 4. The shell, as described above, is almost wholly obscured, except apically at the umbo (U), by the reflected and enlarged middle mantle folds (RM). The outer surface of this fold is actually the inner (because the fold as a whole is reflected) and possesses a number of tentacles and papillae. The inhalant aperture is long, extending from the antero-dorsal tentacle (ADT) to the mid point of the posterior margin of the shell. Inhalant currents (solid arrows) can enter the mantle cavity at all points of this aperture. Conversely, the exhalant flow (open arrow) is confined to a discrete siphon (ES) located

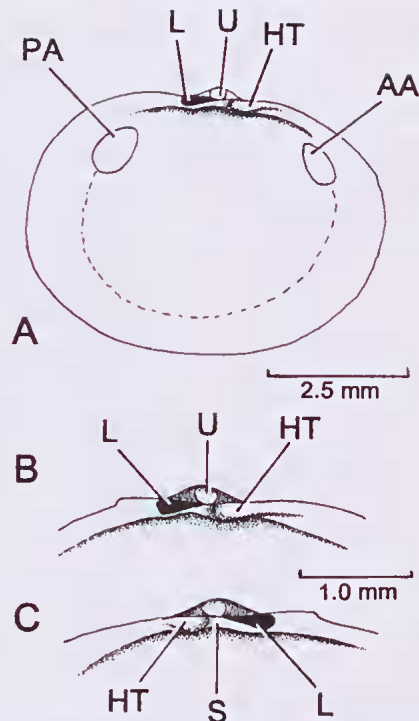


FIG. 3. *Scintillona daviei* sp. nov.: A, internal view of the left shell valve; B, C, internal views of the left and right hinge plates respectively (see Abbreviations section earlier).

beneath the posterior dorsal tentacle (PDT) and is formed by fusion of the inner mantle folds only, that is, type A (Yonge 1982). Anteriorly, where the main inhalant current is located, are three pairs of anterior tentacles (AT) whereas posteriorly there is only one pair (PT). The outer surface of the mantle is adorned by two cycles of papillae above each valve. The outermost cycle approximately tracks the location of the postero-ventral valve margins. The inner cycle defines the mantle edge apically. Also seen in Fig. 4 is the extended foot, comprising a posterior 'heel' (F(H)) and a much longer anterior 'toe' (F(T)) within which is a distinctive red pigment spot (PS). The foot allows *S. daviei* to crawl effectively.

The anatomies of the organs of the mantle cavity of *Scintillona daviei* are illustrated from the left side in Fig. 5. Once again, the inhalant flow is indicated by closed arrows and the exhalant by an open arrow. The homorhabdic, eulamellibranchiate ctenidia are the largest struc-

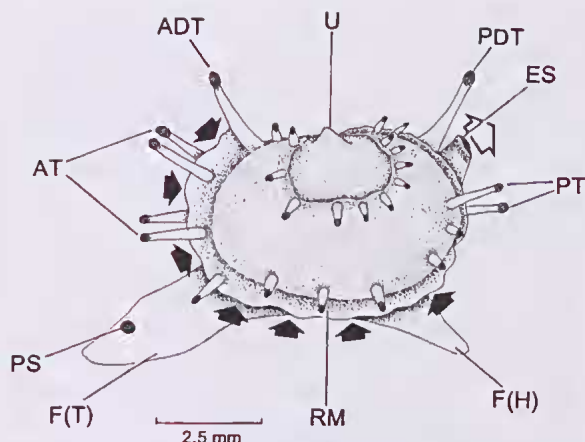


FIG. 4. *Scintillona daviei* sp. nov: individual illustrated from the left side showing the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

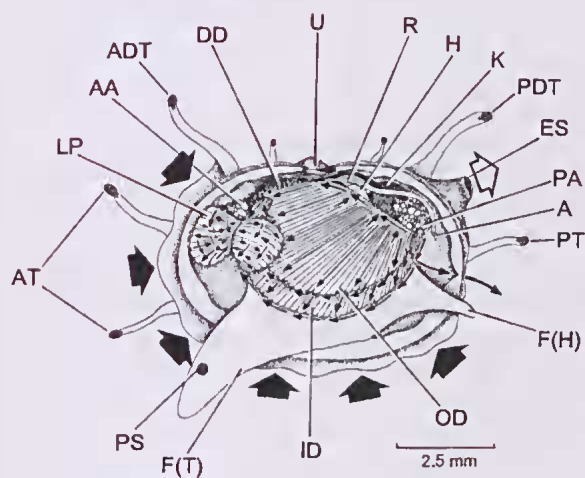


FIG. 5. *Scintillona daviei* sp. nov: structure and ciliary currents of the ctenidia and labial palps, as seen from the left side. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

tures in the mantle cavity and each comprises an inner (ID) and an outer demibranch. The pattern of ciliation on the ctenidia is of type C(1) (Atkins 1937) and thus bears a close resemblance to those of *Galeomma turtoni* (Sowerby, 1825) (Popham 1940), *Divariscintilla maoria* Powell, 1932 (Judd 1971) and *Galeomma takii* (Kuroda, 1945) (Morton 1973a). That is, only the inner demibranch bears a ventral marginal

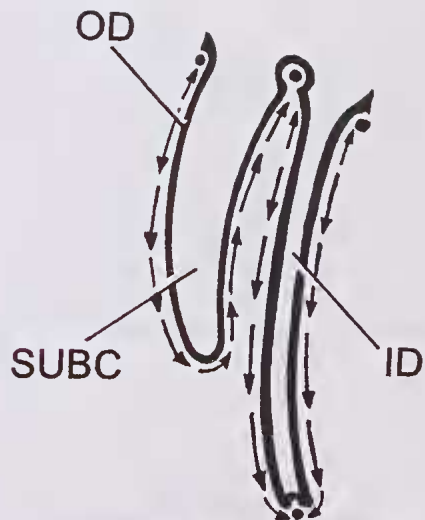


FIG. 6. *Scintillona daviei* sp. nov: diagrammatic transverse section through the right ctenidium showing the ciliary currents and the oral-ward currents (●) (see Abbreviations section earlier).

food groove, although there are other oralward currents in the ctenidial axis and where the ascending lamellae of the inner and outer demibranchs unite with the visceral mass and mantle, respectively. The outer demibranch does not achieve anterior contact with the labial palps. Rather, accepted material passes onto the inner demibranch to be transported to the labial palps. Such a ctenidial-labial palp configuration is typical of the Galeommatoidea and is of Category 3 (Stasek 1964). The labial palps (LP) located anteriorly below the anterior adductor muscle (AA) possess ciliary currents on their grooved inner surfaces that are responsible for the sorting, selection and either acceptance or rejection of potential ctenidially-collected food particles. Rejected material is evicted as pseudofaeces from the infra-branchial chamber of the mantle cavity posteriorly below the exhalant siphon (ES).

The structure and ciliation of the left ctenidium of *Scintillona daviei* are illustrated in transverse section in Fig. 6. The outer demibranch (OD) only, enclosing this component of the supra-branchial chamber (SBC) is modified for the brooding of fertilised eggs and larvae. The longer inner demibranch (ID) is hence the main ciliary potential food transporting structure in *S. daviei*.

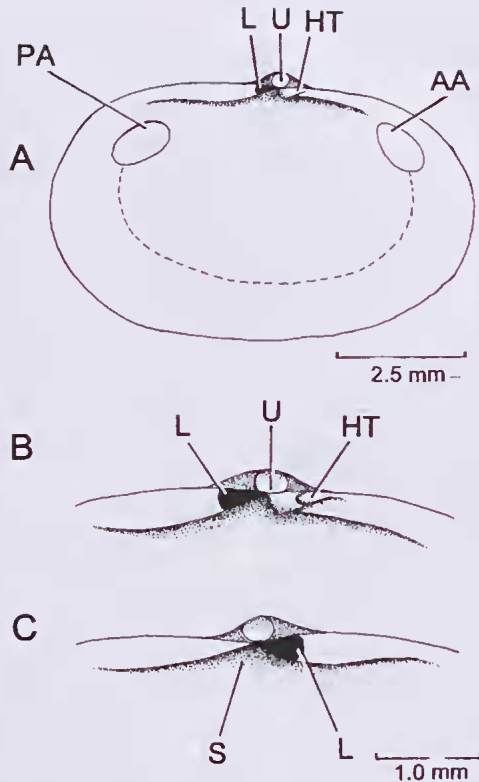


FIG. 7. *Scintilloua cryptozoica*: A, internal view of the left shell valve; B, C, internal views of the left and right hinge plates, respectively (see Abbreviations section earlier).

SHELL STRUCTURE AND ANATOMY OF SCINTILLONA CRYPTOZOICA

The shell of *Scintilloua cryptozoica* has a maximum length of 10 mm and is longer relative to shell height than *S. daviei*. The shell is uniformly translucent white and covered by a very thin (2 μm) periostracum. The shell is also more equilateral than *S. daviei* but is similarly equi-valve. The internal structure of the shell is illustrated in Fig. 7A. The anterior (AA) and posterior adductor (PA) muscles are of approx. equal size and are situated below the anterior and posterior hinge lines, respectively. The hinge plate is illustrated in Fig. 7B & C. The ligament (Fig. 7, L) is situated posterior to the umbo (U) and there is an anterior hinge tooth (HT) in the left valve only (Fig. 7B). There is not a similar hinge tooth in the right valve as there is in *S. daviei*. There is, however, a medial socket (S) directly beneath the umbo.

A mature individual of *Scintilloua cryptozoica* is illustrated in life position in Fig. 8. It is suspended by a single byssal thread (B) from the roof of the crab gallery in the mussel clump. The shell is almost wholly obscured, except apically at the umbo (U), by the reflected and enlarged middle mantle folds (RM). As in *S. daviei*, the outer surface of this fold is actually the inner and possesses a number of tentacles and papillae all of which are tipped deep red. The inhalant aperture is long, extending from the antero-dorsal tentacle (ADT) to the mid point of the posterior margin of the shell. Inhalant currents (solid arrows) can enter the mantle cavity at all points along this aperture. Conversely, the exhalant flow (open arrow) is confined to a discrete siphon (ES) located beneath the posterior dorsal tentacle (PDT) and is formed by fusion of the inner mantle folds only, that is, type A (Yonge 1982). Anteriorly, where the main inhalant current is located, are two (three in *S. daviei*) pairs of anterior tentacles (AT) whereas posteriorly there are four (only one in *S. daviei* sp nov.) pairs (PT). The outer surface of the mantle is adorned by an array of numerous papillae. Also seen in Fig. 8 is the posterior 'heel' of the foot (F(H)). The foot allows *S. cryptozoica* to crawl.

Scintilloua cryptozoica, like *S. daviei*, has a distinctive array of tentacles and papillae adorning the middle mantle folds that are reflected to mostly cover the shell except apically (Fig. 9). The mantle edge is a light red around the exhalant siphon and yellow around the inhalant aperture. There are antero- and postero-dorsal tentacles above the inhalant aperture and exhalant siphon, respectively. In addition, there are two pairs of other tentacles anteriorly and four pairs posteriorly. Smaller papillae adorn the outer (actually the inner) surface of the reflected middle mantle fold. All the tentacles and papillae are coloured a deep red apically. Such an arrangement of tentacles and papillae, the translucent hinge and the absence of a pigment spot in the foot of *S. cryptozoica*, distinguishes it from *S. daviei*.

The anatomies of the organs of the mantle cavity of *Scintilloua cryptozoica* are illustrated from the left side in Fig. 10. Here, the inhalant flow is indicated by closed arrows and the

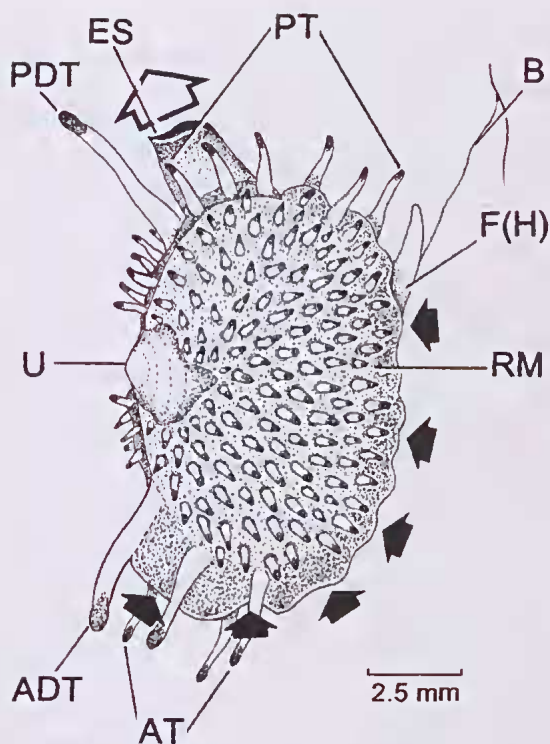


FIG. 8. *Scintillona cryptozoica* illustrated in life position attached to the roof of the gallery made by the crab *Pilumnopus serratifrons* in the clump of *Trichomya hirsuta*. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

exhalant by an open arrow. The homorhabdic, eulamellibranchiate ctenidia are the largest structures in the mantle cavity and each comprise an inner (ID) and an outer demibranch. The outer demibranch is much reduced in comparison with the inner, as in *S. daviei*. Similarly, the ctenidial-labial palp configuration is of Category 3 (Stasek 1964) and the labial palps (LP) located anteriorly below the anterior adductor muscle (AA) possess ciliary currents on their grooved inner surfaces that are responsible for the sorting, selection and either acceptance or rejection of potential ctenidially-collected food particles.

The ciliary currents of the inner surface of the mantle and the visceral mass of *Scintillona cryptozoica* are illustrated in Fig. 11. When viewed from the left side, the ciliary currents of the visceral mass move particles in an anticlockwise direction. That is, dorsally particles are moved by an oralward current that approximates the position of a similarly directed current in the junction of the ascending lamella of the inner demibranch with the visceral mass. Material is then circulated downwards and backwards, to eventually fall from the visceral mass posteriorly and be captured by the currents of the mantle. These move particles in a similar anticlockwise direction on the inner surface of the right mantle lobe (but of course in a clock-

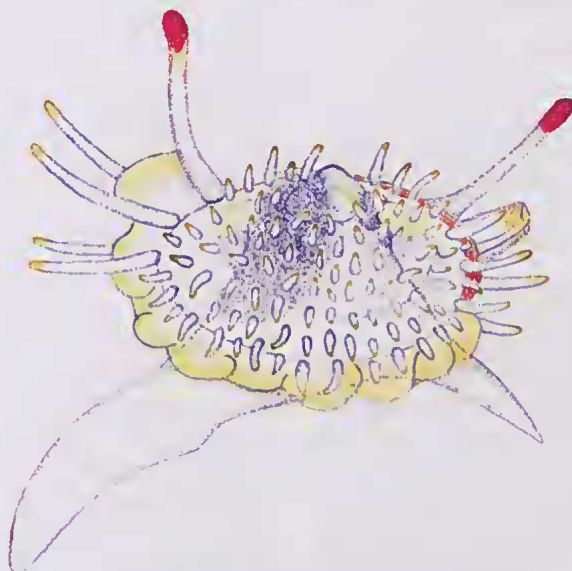


FIG. 9. *Scintillona cryptozoica*: mature individual illustrated from the left side.

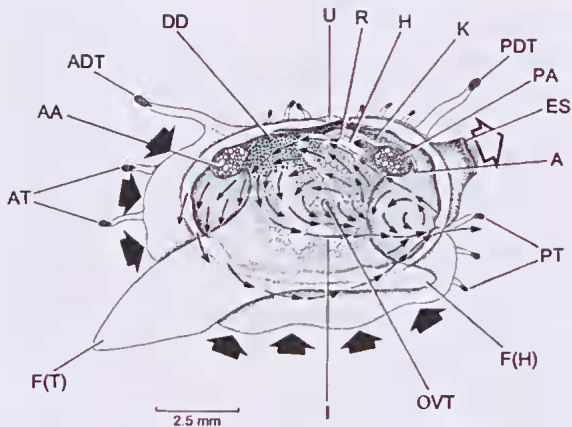


FIG. 10. *Scintilloua cryptozoica*: organs and ciliary currents of the ctenidia and labial palps, as seen from the left side. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

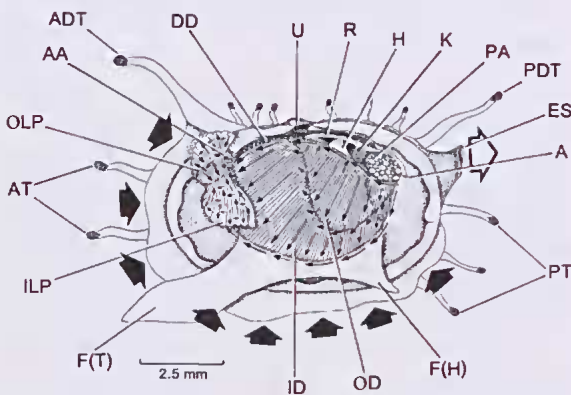


FIG. 11. *Scintilloua cryptozoica*: organs and ciliary currents of the visceral mass. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

wise direction on the left) circulating material from the postero-dorsal region of the mantle cavity forwards but then backwards ventrally. When such a flow arrives posteriorly, held and other captured material rejected by the visceral mass, is discharged from the mantle cavity as pseudofaeces at a point just below the exhalant siphon.

POPULATION STRUCTURES OF SCINTILLONA DAVIEI AND SCINTILLONA CRYPTOZOICA

Of the 100 clusters of *Trichomya hirsuta* that possessed the commensal galeommatids, 40 com-

prised groups of only *Scintilloua cryptozoica*, 27 comprised groups of *S. daviei* and 33 were sympatric. That is, the sympatry is neither 100% nor, obviously, obligatory. Clusters of *S. cryptozoica* and *S. daviei* contained numbers of individuals ranging from 1 to 25 and 1 to 7, respectively.

Figure 11 shows the position of the ovotestis (OVT) in the visceral mass of *Scintilloua cryptozoica*. This has not been examined histologically, but it develops primarily postero-ventrally around the intestine (I). Both species appear to be protandric consecutive hermaphrodites, with the male component of the ovotestis dominating shell length sizes of 1–3 mm (*S. cryptozoica*) and 1–2.5 mm (*S. daviei*), respectively. Females of the two species ranged in shell length from 5–10 mm and 3–7.5 mm, again respectively. Both species brood fertilised eggs in the outer demibranchs only of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm (Fig. 12). It seems that in both *S. cryptozoica* and *S. daviei*, the colour (and its intensity) of the tips of the mantle tentacles and papillae change (and are enhanced) with size which is also related to both age and stage of sexual development (Table 3).

The compositions of the clusters of *Scintilloua cryptozoica* are identified in Table 4. Cluster composition ranged from solitary individuals (x 23) to 25 individuals (x 1). Most individuals were thus in clusters of more than one and an average of 8.7. Solitary individuals comprised but 8.2% of the total population and most of these (16) were in the intersex stage. Significantly, brooding females were never solitary and were recorded from clusters comprising 2, 9 and 14 individuals. That is, they are associated with one or more males which are presumably required to effect fertilisation. The greatest numbers of individuals in the clusters were at the intersex stage and, except for one case of clusters of 14 individuals, these always outnumbered females by a factor of > 2:1 and more often by ~ 6:1. That is, each cluster of more than one individual of *S. cryptozoica* usually comprised a female plus a number (1–6) of intermediate-sized intersex individuals. If a brooding female was also present in the cluster there was also usually a male present. Thus, of the total of 73 clusters of *S. cryptozoica* examined, the average

Table 3. Variations in colour with size in *Scintillona cryptozoica* and *Scintillona daviei*.

Reproductive stage	~Shell length range (mm)	<i>Scintillona cryptozoica</i>	~Shell length range (mm)	<i>Scintillona daviei</i>
Male	1.0–3.0	Both tentacles pale	1.0–2.5	Both tentacles very pale
Intersex	2.0–8.5	Both tentacles pale yellow	2.0–6.0	Both tentacles pale red/purple
Female	5.0–10.0	Posterior tentacle red: anterior paler	3.0–7.5	Posterior tentacle red/purple: anterior paler
Brooding female	6.5–8.0	Both tentacles bright red	3.5–6.0	Both tentacles bright red/purple

Table 4. The composition of the clusters of *Scintillona cryptozoica*.

Cluster size (Nos of individuals)	1	2	3	4	5	6	7	8	9	11	14	18	25	
Numbers of such clusters	23	14	9	7	4	1	2	5	1	1	4	1	1	
Total no. individuals	23	28	27	28	20	6	14	40	9	11	56	18	25	
Cluster composition														
Male	1	2	3	3	–	–	–	1	1	–	5	2	4	22
Intersex	16	14	16	20	17	6	10	33	5	8	15	16	18	194
Female	6	7	8	5	3	–	4	6	2	3	33	–	3	80
Brooding females	–	5	–	–	–	–	–	–	1	–	3	–	–	9

Table 5. The composition of the clusters of *Scintillona daviei* sp. nov.

Cluster size (Nos of individuals)	1	2	3	4	5	6	7	
Numbers of such clusters	23	12	11	5	5	2	1	
Total numbers of individuals	23	24	33	20	25	12	7	
Cluster composition								
Male	3	1	1	–	2	3	–	10
Intersex	12	9	25	10	15	5	7	83
Female	7	7	4	9	3	3	–	33
Brooding females	1	7	3	1	5	1	–	18

cluster of between 8–9 individuals comprised a ratio of 0.30 males: 2.66 intersex individuals: 1.09 females and 0.12 brooding females.

The compositions of the clusters of *Scintillona daviei* are identified in Table 5. Cluster composition ranged from solitary individuals (x 23) to 7 individuals (x 1). Most individuals (61%) were thus in clusters of more than one and an average of 4. Solitary individuals comprised 16.0% of the total population and most of these (12: 52.2%) were in the intersex stage. Brooding

females were never solitary and were recorded from clusters comprising 1–6, but not 7 individuals. Similarly, all cluster sizes, save those comprising 4 and 7 individuals, possessed at least one male. That is, one or more males was always associated with clusters containing mature and brooding females, suggesting, as for *S. cryptozoica*, that a male is required for fertilisation. Also as for *S. cryptozoica*, the greatest numbers of individuals (83: 57.6%) in the clusters were at the intersex stage and always outnumbered

females by an average factor of 2.5:1 and males by often ~8:1. That is, each average cluster of more than one individual usually comprised a female plus a number (~3) of intermediate-sized intersex individuals. If a brooding female was also present in the cluster then so was a male. Of the total of 59 clusters of *S. daviei* examined, therefore, the average cluster of four individuals comprised a ratio of 0.7 males: 0.58 intersex individuals: 0.23 females and 0.12 brooding females.

Both species of *Scintilloua* thus appear to be protandric consecutive hermaphrodites, with the male component of the ovotestis dominating shell length sizes of between 1–3 mm (*S. cryptozoica*) and 1–2.5 mm (*S. daviei*), respectively. Females ranged in shell length from 5–10 mm and 3–7.5 mm for *S. cryptozoica* and *S. daviei*. Both species brood fertilised eggs in the outer demibranchs of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm, again respectively. It seems that the larvae incubated in the female outer demibranchs of both species of *Scintilloua* are released as veligers and after an undefined period of time in the plankton, find a *Pilunnuopeus serratifrons* host gallery in the mussel clumps. There, if a female is in residence, such newly settled juveniles become males. If a female is not present they seem to become of undefined sexuality or 'intersex' and may await, as they grow, further male discovery when they would become females. Fertilised females of both species were the largest individuals in the clusters and it seems possible that following successful brood hatching they die, allowing the next oldest intersex/putative female to mature. There is thus and, as would be expected in such a pattern of reproduction, a dominance in the clusters of both species by intersex/putative females.

DISCUSSION

The two species of *Scintilloua* herein described and discussed are not only clearly related but also at least partially sympatric. Galeommatoidean bivalves are well known associates of marine invertebrates, being recorded from a wide range of phyla (Boss 1965a). Although all galeommatoideans are small as a consequence of their symbiotic lifestyles, species of the Galeommatidae show

great reduction of the shell valves and reflection of the middle fold of the mantle over them (Morton 1973a, 1975). Adoption of a mode of life that can typically best be defined as 'commensal', that is, benefiting from the respiratory currents of the host to facilitate respiration and suspension feeding (Morton 1988) has also been achieved by reproductive specialisation, e.g., the storage (Morton 1980; O'Foighil 1985) of dimorphic sperm (Jespersen *et al.* 2002); simultaneous and consecutive hermaphroditism (Gage 1968a); sexual dimorphism (Jenner & McCrary 1968); self fertilisation (O'Foighil 1987); and even dwarf males (Morton 1976, 1981). *Mysella tunida* (Carpenter, 1864) produces spermatophores to effect fertilisation (O'Foighil 1985), while Mikkelsen & Bieler (1992, fig. 33) described a form of mating behaviour in their new species *Divariscintilla octotentaculata*. *Turtonia minuta* (Fabricius, 1780) produces egg capsules (Oldfield 1963). In the absence of any facilities for histological sectioning of the two species of *Scintilloua* here under consideration, it is unknown if sperm is

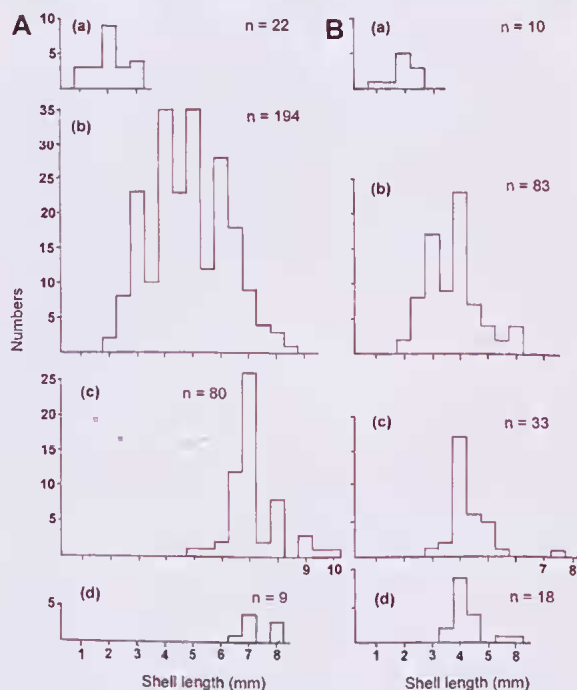


FIG. 12. Shell length histograms illustrating the population structures of: **A**, *Scintilloua cryptozoica*; **B**, *S. daviei* sp. nov. (a) = males; (b) = intersex individuals; (c) = females; and (d) = brooding females.

either stored or is dimorphic: notwithstanding, both species appear to be consecutive protandric hermaphrodites, that is, with newly settled males attracted to females which are then fertilised to produce eggs that are incubated within the outer demibranchs. In two cases, two small males (shell lengths of ~1–1.5 mm) were identified (a) inside the mantle cavity and (b) attached to the byssus of females. Incubation is only to the D-veliger stage, however, no brooded crawl-away juveniles ever being seen.

The males of the two *Scintillona* species are thus not strictly 'dwarf' but probably, as proposed for *Pseudopythina subsinuata* (Lischke, 1871) by Morton (1972), will settle into a clump of adults and become male if an established, maturing female is resident. In the absence of a female, the newly settled individual may become a putative female. This results, as suggested for the present species (Fig. 12), in a surfeit of either putative or intersex females, with each cluster being optimally dominated by one or two mature, possibly gravid or brooding, females. With completion of their life spans, younger females can then assume their places in the cluster hierarchy. Such a pattern of protandric consecutive hermaphroditism has also been identified for *Lepton nitidum* Turton, 1822 (Pelseneer 1925), *Arthritica crassiformis* Powell, 1833 (Morton 1973b), *Montacuta elevata* (Stimpson, 1851) (Verrill & Bush 1898) (Gage 1968a), *Mysella cuneata* (Gage, 1968b), *Montacutona compacta* (Gould, 1861) (Morton 1980).

The situation in *Scintillona cryptozoica* and *S. daviei* species most closely resembles that seen in *Pseudopythina rugifera* (Carpenter, 1864). O'Foighil (1985b) described 'temporary' dwarf males in *P. rugifera*, as was postulated for *P. subsinuata* by Morton (1972), with both authors providing histograms showing small males and larger females.

Morton & Scott (1989) reviewed the commensal, galeommatid bivalves of Hong Kong, identifying 22 species. Lützen & Nielsen (2005), however, recorded 27 species from intertidal reef flats at Phuket (Andaman Sea), Thailand, and over 50 species are known from Japan (Habe 1977, 1981). Very few, however, have been recorded as occurring with crabs. Manning & Morton (1987) reported upon *Fronsella ohshimai* Habe, 1964

[=*Pseudopythina nodosa* (Morton & Scott, 1989)] and *Nipponomysella subtruncata* (Yokoyama, 1922) [= *Barrinysia siphonosomae* (Morton & Scott, 1989)] from Hong Kong living with pinnotherids in the burrows of sipunculan worms. Similarly, few galeommatids are recorded as being sympatric with their hosts. Notwithstanding, Morton & Scott (1989) showed that the shallow water holothurian *Protankyra bidentata* (Woodward & Barrett, 1858) may have three galeommatoids resident with it in Hong Kong, that is, *Pseudopythina ariakensis* (Habe, 1959), *P. tsurumaru* (Habe, 1959) and *Entovalva semperi* Ohshima, 1930. Similarly, Mikkelsen & Bieler (1992) reported upon six species of galeommatoiden bivalves, five of them species of *Divariscintilla* and *Parabornia squillina* Boss, 1965 (Boss 1965b), all living in the burrows of *Lysiosquilla scabricanda* (Lamarck, 1818) in eastern Florida. The five species of *Divariscintilla* were often collected together (see Mikkelsen & Bieler 1992, p. 15 for a description) in a clearly complex sympatric relationship(s). Likewise, in Australian waters, three species of *Ephippodonta*, that is, *E. macdougallii* Tate, 1889, *E. imata* Tate, 1889 and *E. turrubullae* (Buick & Bowden, 1951), along with three other species of *Myllita*, that is, *M. tasmanica* Tenison-Woods, 1875, *M. gemmata* Tate, 1889 and *M. deshayesi* d'Orbigny & Recluz, 1850, as well as an un-named species of *Kellia* can all be found within the burrows of the mud-lobster *Strahlaxinus plectrorhynchus* (Strahl, 1862) (Tate 1889; Matthews 1893; Woodward 1893; Cotton & Godfrey 1938; Buick & Bowden 1951). Finally, Lützen & Nielsen (2005) report that many of the 27 species of galeommatoids they collected from reef flats in Phuket, Thailand, occurred in small (undefined) intra- and inter-specific family 'flocks'.

Although burrowing anomurans and stomatopods are favoured hosts of galeommatoids (Boss 1965a; Mikkelsen & Bieler 1989, 1992), there are few reports of them being associated with crabs. Morton & Scott (1989) described *Pseudopythina macrophthalmenensis* Morton & Scott, 1989, attached to the limbs of the burrowing crab *Macrophthalmus latreillei* (Desmarest, 1817) in Hong Kong, whereas in Okinawa, Japan, it attaches to *M. convexus* Stimpson, 1858 (Kosuge & Itani 1994). Boyko & Mikkelsen (2002) describe *Mysella pedroana* Dall, 1899 attached to the spiny

(also burrowing) anomuran sand crab *Blepharipoda occidentalis* Randall, 1840, often inside the branchial chambers. It was initially suggested by Iredale (1936), that *Scintillona cryptozoica* lives in the burrows made by a species of 'Crangon' (a species of pistol shrimp in the Alpheidae), however although an alpheid, *Alpheus* cf. *pacificus*, was twice collected from the mussel clumps herein examined, only the crab *Pilumnopus serratifrons* was recorded within all the clumps, and it was this species that appeared to be creating the galleries to the roofs of which *S. cryptozoica* and *S. daviei* were attached.

Both species of *Scintillona* are similar to *Ceratomyxia cema* (Narchi, 1966) and *Divariscintilla yoyo* (Mikkelsen & Bieler, 1989) and other species of *Divariscintilla* (Mikkelsen & Bieler 1992), in that they hang by a solitary byssal thread from the roofs of the burrows they inhabit, in the latter cases *Callianassa major* Say, 1818, and the stomatopod *Lysiosquilla scabricauda*. The two species of *Scintillona* herein discussed also possess a complex pattern of large pallial tentacles. The function(s) of the large tentacles are, however, unknown. Such tentacles are absent in some galeommatoidan species, for example, *Scintilla stevensoni* Powell, 1932 (Ponder 1967: fig. 13). In *Rhamphidonta retifera* (Dall, 1899), there are single antero- and postero-dorsal tentacles (Bernard 1975, fig. 2). In the two species of *Galeomma* described by Morton (1973a, 1975), the dorsal tentacles are not only retractable but can autotomise and, in so doing, it was suggested, release a noxious secretion. The complex tentacles of the two species of *Scintillona* are neither retractable nor did they autotomise. Notwithstanding, as with the complex tentacles described for species of *Divariscintilla* Mikkelsen & Bieler (1989, 1992) and for *D. maoria* Powell, 1932, by Judd (1971), they are possibly defensive. That is, they may release a noxious secretion when touched to deter contact from other gallery inhabitants. It is, however, also interesting that the colours of the two species of *Scintillona* deepen with age, and it may be that they also secrete pheromones, as suggested for the yet more complex pallial tentacles of *Chlamydocouclia orcutti* Dall, 1884, by Morton (1981), and in view of the suggestion by Mikkelsen & Bieler (1992) that *Divariscintilla octotentaculata* engages in a 'mating' behaviour.

Another interesting point is that galeommatoidans living in close association with or upon crabs (see above), typically do not have a reflected mantle and hence no pallial tentacles. This is not true however for the two species of *Scintillona* herein discussed that live in galleries created and inhabited by *Pilumnopus serratifrons*, and for their relatives identified above, that live attached to the burrows of anomurans (Boss 1965a). Thus, the possession or lack thereof of pallial tentacles is not wholly related to the category of host, that is, crustacean, worm or other taxon, but to the structure of the galleries or burrows the host creates.

Finally, it is of interest to speculate upon the nature of the relationship between the bivalves and *Pilumnopus serratifrons*. As described above, the degree of sympatry between the two bivalves is not absolute and thus not obligate. However, the associations between the two bivalves with *P. serratifrons* do appear to be obligate, that is, they have never been recorded from clumps of *Trichomya hirsuta* without the crab (unless the crab escaped during handling, but still leaving a definable gallery behind). The bivalves clearly benefit from the protection, that is, aegism as defined by Morton (1988), afforded by living in a gallery underneath a *Trichomya* clump. However, the crab, by virtue of its activities, must aerate its gallery and, in so doing, bring in suspended particulates that the bivalves can exploit. Both species had such particulates in their mantle cavities and intestines. Grutter & Irving (2007) define such an association as facilitation or commensalism. Morton (1988) defines such an association, identified for a number of similar galeommatoidan/host associations from Hong Kong, as commensalism.

ACKNOWLEDGEMENTS

I am grateful to Peter Davie and his colleagues at the Queensland Museum for organising the Thirteenth International Marine Biological Workshop and inviting me to participate. I am also grateful to Lisa Gershwin (James Cook University, Queensland) for allowing me to use her 4-wheel drive vehicle to access the beach herein reported upon. Dr E.M. Harper (University of Cambridge) is thanked for taking the SEM photomicrographs of the *Scintillona* shells. Dr

Peter Middelfart (Australian Museum, Sydney) is thanked for taxonomic advice.

LITERATURE CITED

- Atkins, D. 1937. On the ciliary mechanisms and inter-relationships of lamellibranchs. Part 3. Types of lamellibranch gills and their food currents. *Quarterly Journal of Microscopical Science* **79**: 375–421.
- Bernard, F.R. 1975. *Rhaupludonta* gen. n. from the north-eastern Pacific (Bivalvia, Leptonacea). *Journal de Conchyliologie* **152**: 105–115.
- Boss, K.J. 1965a. Symbiotic erycinacean bivalves. *Malacologia* **3**: 183–185.
- 1965b. A new mollusk (Bivalvia, Erycinidae) commensal on the stomatopod crustacean *Lysiosquilla*. *American Museum Novitates* **2215**: 1–11.
- Boyko, C.B. & Mikkelsen, P.M. 2002. Anatomy and biology of *Mysella pedroana* (Mollusca: Bivalvia: Galeommatoidae), and its commensal relationship with *Blepharipoda occidentalis* (Crustacea: Anomura: Albuneidae). *Zoologische Anzeiger* **241**: 149–160.
- Buick, W.G. & Bowden, W.M. 1951. A new Australian shell. *South Australian Naturalist* **26**: 5–6.
- Cotton, B.C. & Godfrey, F.K. 1938. The Mollusca of South Australia. Part 1. The Pelecypoda. (South Australian Government Printer: Adelaide). 314 pp., 340 figs.
- Davie, P.J.F. 1989a. A re-appraisal of *Heteropauope* Stimpson, and *Pilumnopus* A. Milne Edwards (Crustacea: Decapoda: Pilumnidae) with descriptions of new species and new genera. *Memoirs of the Queensland Museum* **27**(2): 129–156.
- Davie, P.J.F. et al. 1998. *Wild Guide to Moreton Bay. Wildlife and Habitats of a Beautiful Australian Coast – Noosa to the Tweed*. (Queensland Museum: Brisbane). Pp. i–xxiv, 1–408.
- Duke, N.C. 2006. *Australia's Mangroves. The Authoritative Guide to Australia's Mangrove Plants*. (University of Queensland: Brisbane). 200 pp.
- Gage, J. 1968a. The mode of life of *Mysella cuccata*, a bivalve 'commensal' with *Phascolion stroubi* (Sipunculoidea). *Canadian Journal of Zoology* **46**: 919–934.
- 1968b. The mode of life of *Moutacuta elevata*, a bivalve 'commensal' with *Chlyneuella torquata* (Polychaeta). *Canadian Journal of Zoology* **46**: 877–897.
- Grutter, A.S. & Irving, A. D. 2007. Positive interactions in marine communities. Pp. 110–137. In, Connell, S.D. & Gillanders, B.M. (Eds), *Marine Ecology*. (Oxford University Press: Oxford).
- Habe, T. 1977. *Systematics of Mollusca in Japan: Bivalvia and Scaphiropoda*. (Hokuryukan Publishing Company, Ltd.: Tokyo, Japan).
1981. A catalogue of molluscs of Wakayama Prefecture, the Province of Kii. *Publications of the Seto Marine Laboratory, Special Publications Series* **7**: 1–301.
- Hedley, C. 1917. Studies on Australian Mollusca. Part XIII. *Proceedings of the Linnæan Society of New South Wales* **41**: 680–719.
- Iredale, T. 1931. Australian molluscan notes, No. 1. *Records of the Australian Museum* **18**(4): 201–235, pls 22–25.
1936. Australian molluscan notes, No. 2. *Records of the Australian Museum* **19**(5): 267–340.
- Jenner, C.E. & McCrary, A.B. 1968. Sexual dimorphism in erycinacean bivalves. *American Malacological Union, Annual Report* **35**: 43.
- Jespersen, A., Lutzen, J. & Morton, B. 2002. Ultra-structure of dimorphic sperm and seminal receptacle in the hermaphrodites *Barrinysia siphonousouae* and *Pseudopythina ochetostomae* (Bivalvia, Galeommatoidae). *Zoomorphology* **121**: 159–172.
- Judd, W. 1971. The structure and habits of *Divariscitilla maoria* Powell (Bivalvia: Galeommatidae). *Proceedings of the Malacological Society of London* **39**: 343–354.
- Knudsen, J. 1944. A gephyrian, a polychaete and a bivalve (*Jousseaumiella concharuum*, nov. sp.) living together (commensalistically) in the Indo-Malayan seas. *Videnskabelige Meddelelser fra Dansk naturhistorik Forening i Kjobenhavn* **108**: 15–24.
- Kosuge, T. & Itani, G. 1994. A record of the crab associated bivalve, *Pseudopythina macroplutaluensis* from Iriomote Island, Okinawa, Japan. *Veenus* **53**: 241–244.
- Lamprell, K. & Healy, J. 1998. *Bivalves of Australia. Volume 2*. (Backhuys Publishers: Leiden).
- Lützen, J. & Nielsen, C. 2005. Galeommatid bivalves from Phuket, Thailand. *Zoological Journal of the Linnæan Society* **144**: 261–308.
- Manning, R.B. & Morton, B. 1987. Pinnotherids (Crustacea: Decapoda) and leptonaceans (Mollusca: Bivalvia) associated with sipunculan worms in Hong Kong. *Proceedings of the Biological Society of Washington* **100**(3): 543–551.
- Matthews, E.H. 1893. On the habit of the genus *Ephippodonta* (Tate). *Conchologist* **2**: 144–145.
- Mikkelsen, P.M. & Bieler, R. 1989. Biology and comparative anatomy of *Divariscitilla yoyo* and *D. troglodytes*, two new species of Galeommatidae (Bivalvia) from stomatopod burrows in eastern Florida. *Malacologia* **31**: 1–21.
1992. Biology and comparative anatomy of three new species of commensal Galeommatidae with a possible case of mating behavior in bivalves. *Malacologia* **34**: 1–24.

- Morton, B. 1972. Some aspects of the functional morphology and biology of *Pseudopythina subsinuata* (Bivalvia: Leptonacea) commensal on stomatopod crustaceans. *Journal of Zoology, London* **166**: 79-96.
- 1973a. The biology and functional morphology of *Galeomma (Paralepida) takii* (Bivalvia: Leptonacea). *Journal of Zoology, London* **169**: 133-150.
- 1973b. Some factors influencing the location of *Arthritica crassiformis* (Bivalvia: Leptonacea) commensal upon *Anchomasa similis* (Bivalvia: Pholadidae). *Journal of Zoology, London* **170**: 463-473.
1975. Dymantic display in *Galeomma polita* Deshayes (Bivalvia: Leptonacea). *Journal of Conchology* **28**: 365-369.
1976. Secondary brooding of temporary dwarf males in *Ephippodonta (Ephippodontina) oedipus* n. sp. (Bivalvia: Leptonacea). *Journal of Conchology* **29**: 31-39.
1980. Some aspects of the biology and functional morphology (including the presence of a ligamental lithodesma) of *Montacutona compacta* and *M. olivacea* (Bivalvia: Leptonacea) associated with coelenterates in Hong Kong. *Journal of Zoology, London* **192**: 431-455.
1981. The biology and functional morphology of *Chlamydoconcha orcutti* Dall with a discussion on the taxonomic status of the Chlamydoconchacea (Mollusca: Bivalvia). *Journal of Zoology, London* **195**: 81-122.
1988. *Partnerships in the Sea: Hong Kong's Marine Symbioses*. (Hong Kong University Press, Hong Kong). Pp. i-xv + 124.
- Morton, B. & Lutzen, J. 2008. *Loxothylacus spinulosa* (Crustacea: Cirripedia: Rhizocephala) parasitising *Pilumnopus serratifrons* (Decapoda: Pilumnidae) in Moreton Bay, Queensland, Australia. In: Davie, P.J.F. & Phillips, J.A. (Eds), Proceedings of the Thirteenth International Marine Biological Workshop: the Marine Flora and Fauna of Moreton Bay, Queensland, Australia. *Memoirs of the Queensland Museum - Nature* **54**(1): 257-260.
- Morton, B. & Scott, P.H. 1989. The Hong Kong Galeommatacea (Mollusca: Bivalvia) and their hosts, with descriptions of new species. *Asian Marine Biology* **6**: 129-160.
- Narchi, W. 1966. The functional morphology of *Ceratobornia cema*, new species of the Erycinacea (Mollusca: Eulamellibranchiata). *Anais da Academia Brasileira de Ciências* **38**: 513-524.
- O'Foighil, D. 1985a. Sperm transfer in the brooding bivalve *Mysella tumida*. *Biological Bulletin* **169**: 602-614.
- 1985b. Form, function and origin of temporary dwarf males in *Pseudopythina rugifera* (Carpenter, 1864) (Bivalvia: Galeommatacea). *The Veliger* **27**: 245-252.
1987. Cytological evidence for self fertilization in *Lasaea subviridis* (Galeommatacea: Bivalvia). *International Journal of Invertebrate Reproduction and Development* **12**: 83-90.
- Oldfield, E. 1963. Reproduction and development of some members of the Erycinidae and Montacutidae (Mollusca, Eulamellibranchiata). *Proceedings of the Malacological Society of London* **36**: 79-120.
- Pelseneer, P. 1925. Un Lamellibranche commensal de Lamellibranche et quelques autres Lamellibranches commensaux. *Trav Station Zoologie Wimmereux* **9**: 164-182.
- Ponder, W.F. 1967. Observations on the living animal and mode of life of some New Zealand erycinacean bivalves. *Transactions of the Royal Society of New Zealand, Zoology* **10**(3): 21-32.
- Popham, M.L. 1940. The mantle cavity of some of the Erycinidae, Montacutidae and Galeommatidae with special reference to the ciliary mechanisms. *Journal of the Marine Biological Association of the United Kingdom* **24**: 549-586.
- Spärck, R. 1931. *Cycladoconcha amboinensis* n. gen. n. sp., a commensalistic lamellibranch. *Videnskabelige Meddelelser fra Dansk naturhistorik Forening i Kjobenhavn* **91**: 227-240.
- Stasek, C.R. 1964. Synopsis and discussion of the association of ctenidia and labial palps in the bivalved Mollusca. *The Veliger* **6**: 91-97.
- Tate, R. 1889. Description of some new species of marine Mollusca from South Australia and Victoria. *Transactions, Proceedings and Reports of the Royal Society of South Australia* **11**: 60-66.
- Woodward, M.F. 1893. On the anatomy of *Ephippodonta macdougalli*. *Proceedings of the Malacological Society of London* **1**: 20-26.
- Yonge, C.M. 1982. Mantle margins with a revision of siphonal types in the Bivalvia. *Journal of Molluscan Studies* **48**: 102-103.